Morphology of the Brain of Crayfish, Crabs, and Spiny Lobsters: A Common Nomenclature for Homologous Structures

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Abstract. The morphologies of the cerebral ganglia (brains) of three infraorders of the decapod crustaceans (Astacura-crayfish; Brachyura-crabs; Palinura-spiny lobsters) are described. A common nomenclature is proposed for homologous nerve roots, brain regions, tracts, commissures, neuropils, and cell body clusters.

Introduction

Decapod crustaceans have been favored animals among neurobiologists for many years because they are comparatively large arthropods, have well-organized nervous systems and interesting behavior patterns ranging from reflexes to complex social interactions. Several fixed action patterns concerned with protection or escape are mediated by particularly well-defined sensory inputs and large neuromuscular systems, and, much research has been focused on these. The crayfish ventral nerve cord survives well in isolation and has also been exploited in the study of many aspects of the neurophysiology of the ventral ganglia (*e.g.,* Hoyle, 1977; Atwood and Sandeman, 1982; Wine and Krasne, 1982; Wiese *et al.,* 1990).

There is a growing interest, however, in the cerebral ganglia (brains) of the crustaceans. Initial studies on the brains of the spiny lobsters by Maynard in the 1960's (Maynard, 1962; Maynard, 1966; Maynard, 1969; Maynard and Sallee, 1970) came to an untimely end, but the description of the impulse traffic between the eye and the brain was continued by Wiersma and his colleagues

(Wiersma *et al.,* 1982; Glantz and Pfeiffer-Linn, 1990) and the endocrine systems in the eyestalks have been particularly well investigated (Cooke and Sullivan, 1982; Arechiga *et al.,* 1990). The development of a semi-isolated preparation of the crab and then crayfish brain allowed the investigation of eye withdrawal, statocyst driven reflexes, chemoreceptive responses, and antenna II reflexes (Sandeman, 1969, 1971, 1989; Sandeman and Okajima, 1972; Silvey and Sandeman, 1976; Ache and Sandeman, 1980; Sandeman and Wilkens, 1982). Recently there has been a renewed interest in the crustacean cerebral ganglion, stimulated by more detailed anatomical studies and the description of a number of neuronal systems revealed by antibodies raised against various neurotransmitters and neuromodulators (see Wiese *et al.,* 1990).

The entry of researchers from many different fields into crustacean brain research has been accompanied by a certain confusion about the names of different parts of the brain. This confusion is probably the result of a large literature on the brains of the crustaceans, not all of which belonged to the decapods. Within the decapods, problems have been caused by various interpretations of the works of previous authors, and by the earlier authors themselves changing their minds about what to call a particular neuropil (*e.g.,* Hanström, 1924, 1925; 1947). Many recent descriptions of the brains of various decapods have perpetuated the errors or misconceptions of the earlier authors. Progress toward a standard nomenclature for the component neuropils, tracts, and cell bodies of the decapods was made by Tsvileneva and Titova (1985) who adopted the original nomenclature of Helm (1928) in their description of the brains of the crayfish and crab.

The larger decapod crustaceans have life spans of many years and a brain that, in size and complexity, lies somewhere between the octopus and insects. Indications are that the brain and behavior of the crustaceans will attract considerable attention in the future (Wiese *et al.*, 1990). It is therefore timely that a nomenclature for brain morphology of the decapods be compiled for the commonly used species. In this report we suggest names for homologous components (*i.e.*, nerve roots, neuropils, tracts, and groups of cell bodies) that can be recognized in the brains of three infraorders of the decapod Crustacea; the Astacura (clawed lobsters and crayfish), Brachyura (crabs), and Palinura (spiny lobsters). We have chosen representatives from these infraorders because preparations already exist for the physiological investigation of the brains of these animals, and further studies will therefore most likely be done on them.

In selecting names for the various components we have sought, where possible, to keep terms that have been commonly used and to prefer names that do not imply function unless this has been clearly established. We have tried to remove ambiguities and show that the same components can be identified in the three different infraorders. We have included an Appendix which lists synonyms that have been used by other authors for the neuropil areas and cell body clusters we describe. Earlier authors have used the terms "lobe", "body", and "bridge" for several particularly clearly delineated neuropils. Although we prefer the term "neuropil," we have retained these terms as they are well entrenched in the literature on comparative studies of arthropod brains. We do not pretend that our system of nomenclature will apply to all members of the Phylum Crustacea, given their diversity and the very different morphology of the cerebral ganglia of some forms (Elofsson and Hessler, 1990).

Material and Methods

Brain morphologies of the three different types of decapod were compiled from serial sections of wax embedded and silver impregnated, or plastic embedded and osmium ethyl gallate stained material. *Cherax destructor* has been taken as the representative of the Astacura, *Scylla serrata* of the Brachyura, and *Jasus novaehollandiae* and *Panulirus argus* of the Palinura.

Results

Head Appendages

Several terms are used for the two pairs of antennae. We believe the most unambiguous to be antenna I and antenna II. Antenna I is equivalent to the antennule or first antenna, and antenna II to antenna or second antenna, terms that we also use.

Antenna I (ANT I): Basal segments contain the statocysts and muscles, and bear two sensory flagella both of which carry mechanoreceptive and chemoreceptive sensilla (Derby, 1982; Derby and Ache, 1984). The lateral flagellum bears special olfactory sensilla; the aesthetasc sensilla (Grünert and Ache, 1988).

Antenna II (ANT II): Basal segments contain muscles and bear a scale-like structure and a single long sensory flagellum carrying both mechanoreceptive and chemoreceptive sensilla (Tazaki and Shigenaga, 1974; Derby, 1982).

Nerve Roots

We define the nerve roots as those bundles of axons that extend from the brain or other central nervous ganglia and contain either sensory afferents, motor efferents, or both, but not interneurons. The tract of axons between the brain and the optic ganglia in the eyestalk is, therefore, not a nerve root because it forms a connection between central ganglia.

Anterior median nerve (AMNv): This short nerve bundle projects from the anterior surface of the brain and supplies the muscles of the median segment of the eyestalk. There is no information on afferents in this nerve bundle.

Oculomotor nerve (OMNv): The oculomotor nerve carries motor neurons to the muscles of the eyestalk. It also contains primary afferent axons from mechanoreceptors in this area. Motor neurons to some eye muscles have been found in the lateral protocerebral tract in crabs (Sandeman, 1964) and crayfish (Mellon, 1977).

Antenna I nerve (A_INv): Motor neurons to the muscles in the basal segments of antenna I are contained in this nerve together with the primary afferents from the receptors on the flagella and basal segments. To the best of our knowledge, all axons from the olfactory sensilla (aesthetascs) diverge from the main bundle and project exclusively to the olfactory lobe (see below) (Sandeman and Denburg, 1976; Mellon and Munger, 1990; Schmidt and Ache, 1990; Schmidt and Ache, 1992), non-aesthetasc chemosensory and mechanosensory afferents project to the lateral and median antenna I neuropil (Roye, 1986; Schmidt and Ache, 1990; Roye and Bashor, 1991; Schmidt *et al.*, 1992).

Antenna II nerve (A_{II}Nv): Motor neurons to the muscles in the basal segments of antenna II run in this nerve together with primary afferents from mechanoreceptors, proprioceptors, and chemoreceptors on the flagellum and the basal segments. All axons terminate in the same neuropil (see below). A number of subdivisions of the antenna II nerve for crayfish have been described (Habig and Taylor, 1982; Sandeman and Wilkens, 1982; Tautz and Müller-Tautz, 1983).

Tegumentary nerve (TNv): This is a purely sensory nerve carrying primary afferents from mechanoreceptors

and other sensilla ⟨⟩ ⟨⟩ ⟨⟩ dorsal carapace (Kinnamon, 1979).

Posterior ⟨⟩ ⟨⟩ *e* (PMNv): Projecting from the posterior of ⟨⟩ ⟨⟩ he median nerve carries interneurons betw⟨⟩ ⟨⟩ ⟨⟩ ⟨⟩ ain and the oesophageal ganglion.

Brain ⟨⟩ *ons and Neuropils (Fig. 1)*

There are three main divisions of the brain, protocerebrum, deutocerebrum, and tritocerebrum, reflecting the three ganglia that have fused to form it. The neuropils of the optic ganglia and lateral protocerebrum are located in the eyestalks of crayfish, crabs, and lobsters. The median protocerebrum and tritocerebrum are located medially.

Protocerebrum

The protocerebrum can be conveniently subdivided into three parts, the optic ganglia, the lateral protocerebrum and the median protocerebrum.

OPTIC GANGLIA. Contains three neuropils that are probably devoted to processing the information received by the photoreceptors of the retina.

Lamina (L): The first neuropil behind the retina, the lamina is geometrically structured.

External medulla (EM): Lying directly behind the lamina, the external medulla is similarly geometrically structured, but is also transversely layered.

Internal medulla (IM): The most proximal of the three neuropils in the optic ganglia, this too is geometrically organized and has clearly defined transverse bands.

LATERAL PROTOCEREBRUM. Contains two neuropils. In crayfish, crabs, and spiny lobsters the neuropils of the lateral protocerebrum lie in the distal segment of the eyestalk, directly proximal to the optic ganglia. In some anomurans the lateral protocerebrum is incorporated into the centrally located median protocerebrum.

Terminal medulla (TM): This complex neuropil is not geometrically organized but has a number of subdivisions (Blaustein *et al.*, 1988). It contains neurosecretory cells of the X-organ and its associated neurohaemal organ, the sinus gland, which together constitute one of the most important neuroendocrine systems in the crustaceans.

Hemiellipsoid body (HN): Positioned anterior to the terminal medulla, this neuropil sometimes has a glomerular structure, and is large and layered in some anomurans, a characteristic which led Hanström (1925) to postulate that it is homologous with the corpora pedunculata of the insects.

MEDIAN PROTOCEREBRUM. Forms the anterior part of the medially situated neuropils of the brain. It contains two paired medial and two unpaired median neuropils. (Throughout this paper we use the term *median* to describe a structure that straddles the midline, and *medial* to describe paired structures near or at the midline. Thus
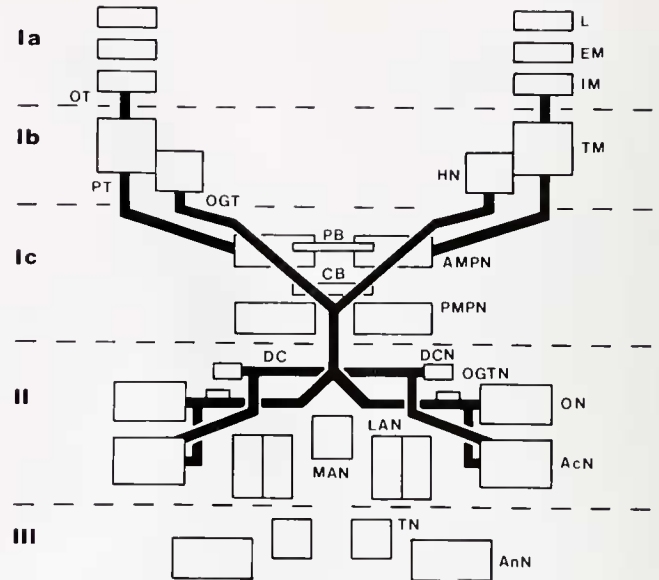

Figure 1.   Brain regions and neuropils that can be identified in all three brain types and that are considered to be homologous. Heavy black bars represent the tracts and commissures linking the neuropil areas, shown as boxes. The roman numerals represent the divisions of the brain according to the way we have arranged them in the text of the paper: *i.e.,* I = protocerebrum (with three subsections); II = deutocerebrum; III = tritocerebrum. A key to the abbreviations is provided in Appendix 2.

the *median* protocerebrum is made up of two anterior *medial* protocerebral neuropils and two posterior *medial* protocerebral neuropils). While clearly discernible in some section planes, these four neuropils tend to fuse with one another dorsally and ventrally, making the distinction between them somewhat arbitrary. No primary afferent projections to the neuropils of the median protocerebrum have been reported.

Anterior medial protocerebral neuropil (AMPN): These two neuropils lie on each side of the midline at the anterior of the median protocerebrum.

Posterior medial protocerebral neuropil (PMPN): These two neuropils lie on each side of the midline, directly posterior to the anterior medial protocerebral neuropils.

Protocerebral bridge (PB): Embedded in the anterior edge of the anterior medial protocerebral neuropil, this V-shaped neuropil has a characteristic form containing many large through-running axons with fine side branches. In the crayfish *Cherax*, extra-retinal photoreceptors lying in the anterior of the brain terminate in the neuropil of the protocerebral bridge (Sandeman *et al.*, 1990).

Central body (CB): A cigar-shaped neuropil lying across the brain and dividing the anterior from the posterior medial protocerebral neuropils. The central body is a well-defined area of neuropil that immunocytochemical studies have shown to contain a wide variety of different neuroactive substances (Schürmann *et al.*, 1991).
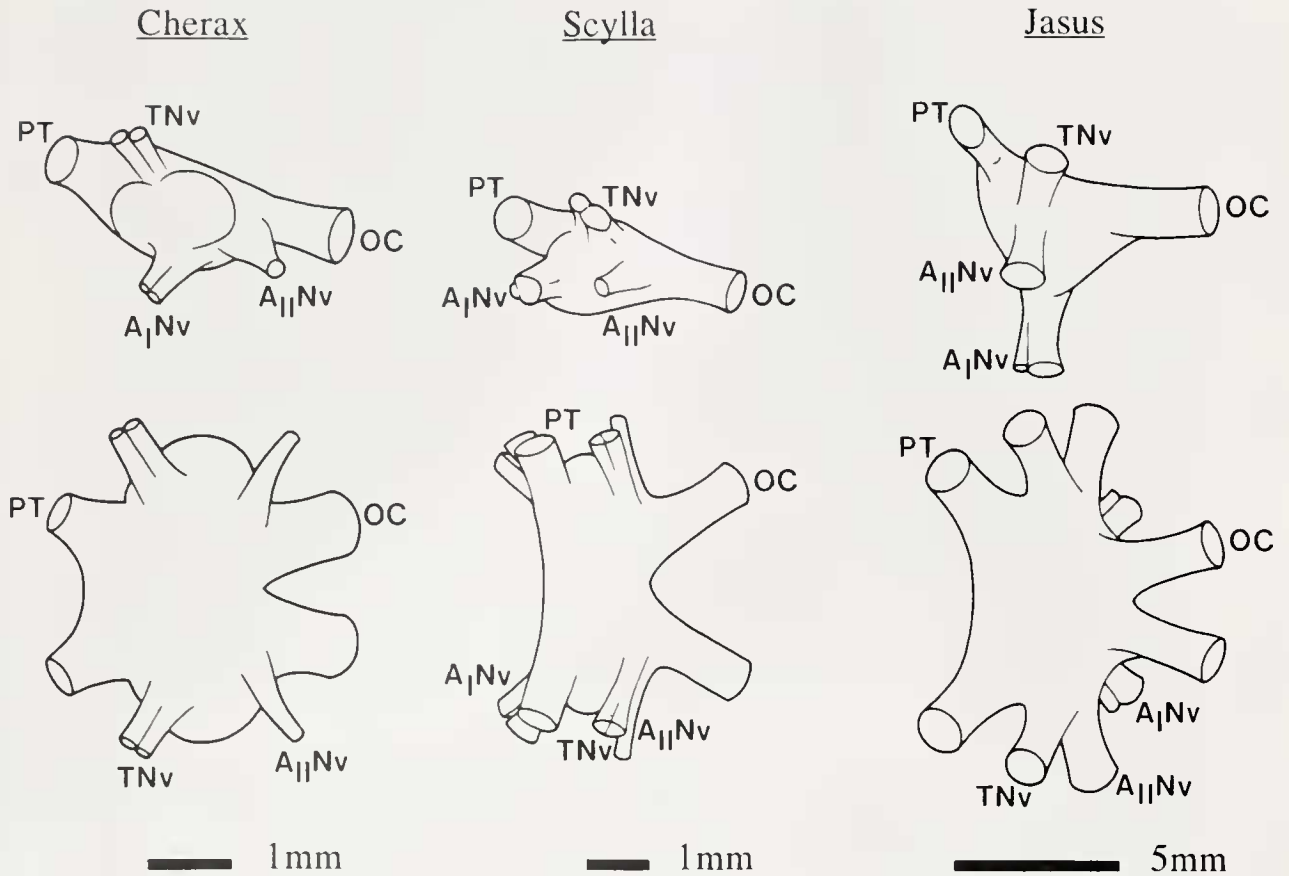
Cherax   Scylla   Jasus

Figure 2. Camera lucida-traced outlines of the brains of *Cherax, Scylla* and *Jasus* seen from the side and from above. Anterior is to the left of the page. In the crayfish and crab, the oesophageal connectives and the protocerebral tract lie in nearly the same horizontal plane. In the spiny lobster the protocerebral tracts extend upwards, almost at right angles to the plane of the oesophageal connectives. Antenna 1 and antenna 2 nerve roots of the crayfish and the crab point anteriorly and ventrally, whereas those of the spiny lobster project almost directly ventrally. These differences are reflected in the organization of the neuropils within the brains of the three animals.

Deutocerebrum

Olfactory lobe (ON): The olfactory lobes are clearly delineated spheres lying on each side of the brain. They contain cone-shaped areas of densely packed synaptic fields—the olfactory glomeruli—arranged with their apices pointing to the center of the sphere. The olfactory lobes receive the primary afferent endings of the chemoreceptors on antenna I (Sandeman and Denburg, 1976; Mellon and Munger, 1990; Schmidt and Ache, 1990; Schmidt and Ache, 1992).

Lateral antenna I neuropil (LAN): Consisting of two clear subdivisions when viewed in frontal sections, the lateral antenna I neuropil on each side of the brain receives afferents from mechanoreceptors, statocysts, and non-aesthetasc chemoreceptors from the ipsilateral antenna I (Sandeman and Denburg, 1976; Yoshino *et al.*, 1983; Roye, 1986; Blaustein *et al.*, 1988; Schmidt and Ache, 1990). It also contains the synaptic fields of the motor

neurons that control the movements of the ipsilateral antenna 1 (Roye and Bashor, 1991; Schmidt *et al.*, 1991). The lateral antenna 1 neuropils have sometimes been referred to as "parolfactory lobes" (see Appendix 1).

Median antenna I neuropil (MAN): A relatively diffuse block of neuropil that lies across the brain between or dorso-anterior to the lateral antenna I neuropils. The median antenna I neuropil fuses anteriorly with the posterior medial protocerebral neuropils, and posteriorly with the tegumentary and antenna II neuropils. Little is known about the projections to this area of the brain. Branches of descending interneurons related to statocyst inputs extend into the medial antenna I neuropil in both crabs (Fraser, 1974) and crayfish (Yoshino *et al.*, 1983). In the blue crab, mechanosensory afferents from sensilla at the base of antenna I project to the medial antenna I neuropil, where antenna I motorneurons also branch (Roye, 1986; Roye and Bashor, 1991). Primary afferents from the base

of the antennule ha... ...en observed that project to the medial antenna ... ...il in spiny lobsters (Schmidt, unpub. obs.).

Access... ...N): The accessory lobes lie directly posteric... ...al to the olfactory lobes. They are larger than th... ...ory lobes in the crayfish, about the same size as the olfactory lobes in spiny lobsters, and very much smaller than the olfactory lobes in crabs. They contain large numbers of small round glomeruli. In the spiny lobster, the accessory lobes are subdivided into medial, central, and lateral layers containing glomeruli of different sizes (Maynard, 1966, 1971; Blaustein *et al.*, 1988). The accessory lobes do not appear to receive a direct input from primary afferent axons, nor have motor efferents been found that have their synaptic fields there.

Deutocerebral commissure neuropil (DCN): Small round ventrally situated neuropils characterized by receiving strong projections from the deutocerebral commissure and from the medial protocerebrum. Clearly defined in crayfish and spiny lobsters with large deutocerebral commissures, these neuropils have not yet been identified in the crab brain. No primary afferent inputs are known that project to the deutocerebral commissure neuropils, nor has the nature of the interneuronal input been defined. The subject of much confusion, these neuropils have been called "parolfactory lobes" in several recent publications (Tsvileneva and Titova, 1985; Sandeman *et al.*, 1988; Blaustein *et al.*, 1988) and are renamed here in accordance with our policy to avoid functional names where we can. See Appendix 1 for synonyms.

Olfactory globular tract neuropil (OGTN): First pictured in crayfish by Helm (1928) and labelled "z", attention was again drawn to this neuropil by Tsvileneva and Titova (1985). It appears to lie within, or very closely associated with, the olfactory globular tract at a point just before the tract reaches the olfactory and, when present, accessory lobes. Present also in crabs, this neuropil has assumed a greater significance since the branches of large serotonin immunoreactive neurons, associated with the accessory and olfactory lobes, have been found in this neuropil (Sandeman and Sandeman, 1987; Beltz *et al.*, 1990; Schmidt *et al.*, 1991). Connections between the olfactory globular tract neuropil and other parts of the nervous system have yet to be determined.

Tritocerebrum

Antenna II neuropil (AnN): These cylindrical neuropils are posterior to the accessory lobes in crayfish, posterior to the olfactory lobes in crabs, and postero-dorsal to the olfactory lobes in the spiny lobster. They are tapered laterally and often have a geometrically arranged pattern of axons running antero-posteriorly across them. The primary afferents from antenna II end in the antenna II neuropil which also contain the synaptic fields of the motor neurons that control the movements of antenna II (Sandeman and Wilkens, 1982; Habig and Taylor, 1982; Tautz and Müller-Tautz, 1983).

Tegumentary neuropil (TN): Each tegumentary nerve, carrying the afferent input from the dorsal carapace (Sandeman, 1969; Kinnamon, 1979), ends in a tight knot of neuropil dorsal and somewhat anterior to the medial margin of the antenna II neuropil.

Tracts and Commissures (Fig. 1)

Many tracts in the brains of the crustaceans link areas of neuropils, and a number of axon bundles cross the brain. We have restricted ourselves here to the largest and best known that can be unequivocally identified, when present, in the three infraorders.

Optic tract (OT): The optic tract links the last of the optic ganglia (internal medulla) to the lateral protocerebrum. Very short in the astacurans, brachyurans, and palinurans, it is often confused with the much longer protocerebral tract that links the terminal medulla to the median protocerebrum in these groups.

Protocerebral tract (PT): Axons in this tract link the terminal medulla and hemiellipsoid body with the anterior medial protocerebral neuropil and other areas of the brain. Sometimes inaccurately referred to as the "optic nerve" or "optic tract" (see Appendix 1).

Olfactory globular tract (OGT): The olfactory globular tract links the hemiellipsoid bodies and terminal medullae with the olfactory and accessory lobes on both sides of the brain by crossing the brain just dorsal to the central body neuropil. It typically contains very large numbers of small diameter axons (1 μm and less).

Deutocerebral commissure (DC): This commissure is large in crayfish and spiny lobsters, but cannot be identified with certainty in crabs. In crayfish it contains two populations of axon diameters that cross the brain between the two accessory lobes.

Oesophageal connectives (OC): These two large tracts link the brain with the suboesophageal ganglion and the ventral cord.

Cell Body Clusters

Homologous cell bodies are more difficult to identify than neuropils, tracts, and commissures. In some cases, such as the cells associated with the olfactory and accessory lobes, the cell bodies can be identified by their characteristic morphology, but in others there are no such criteria available. The projections of the primary neurites of a few cell bodies are known, but these are in the minority, and then information is often available for only one brain type.
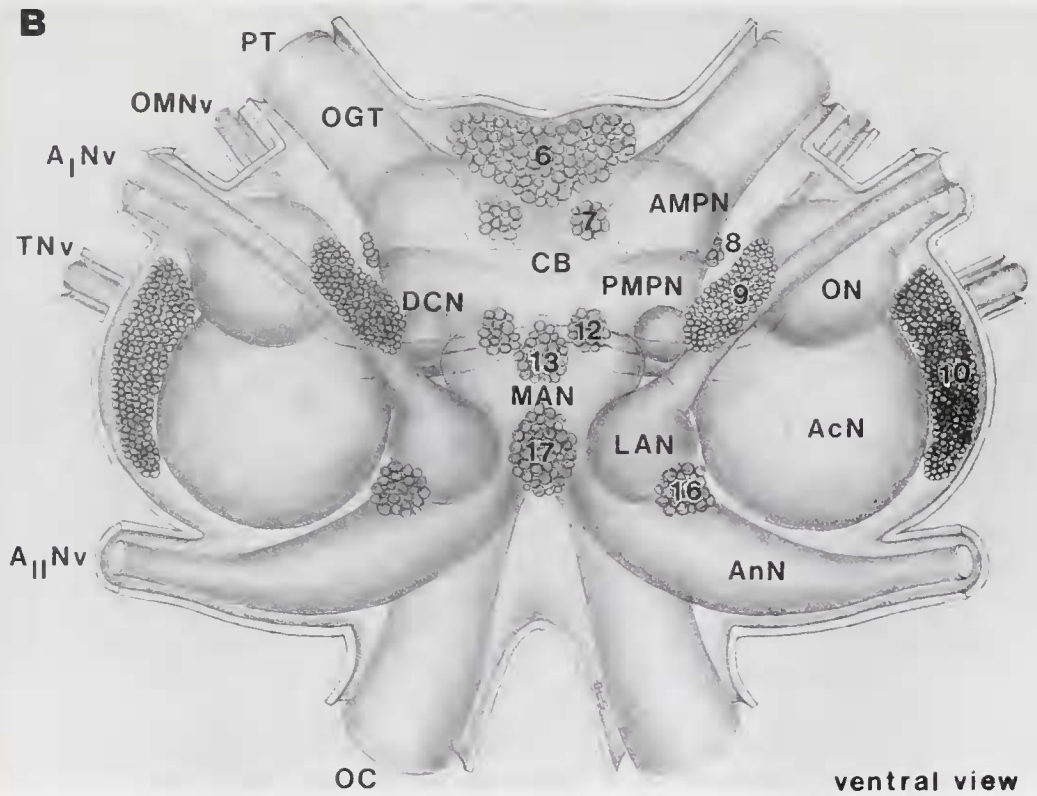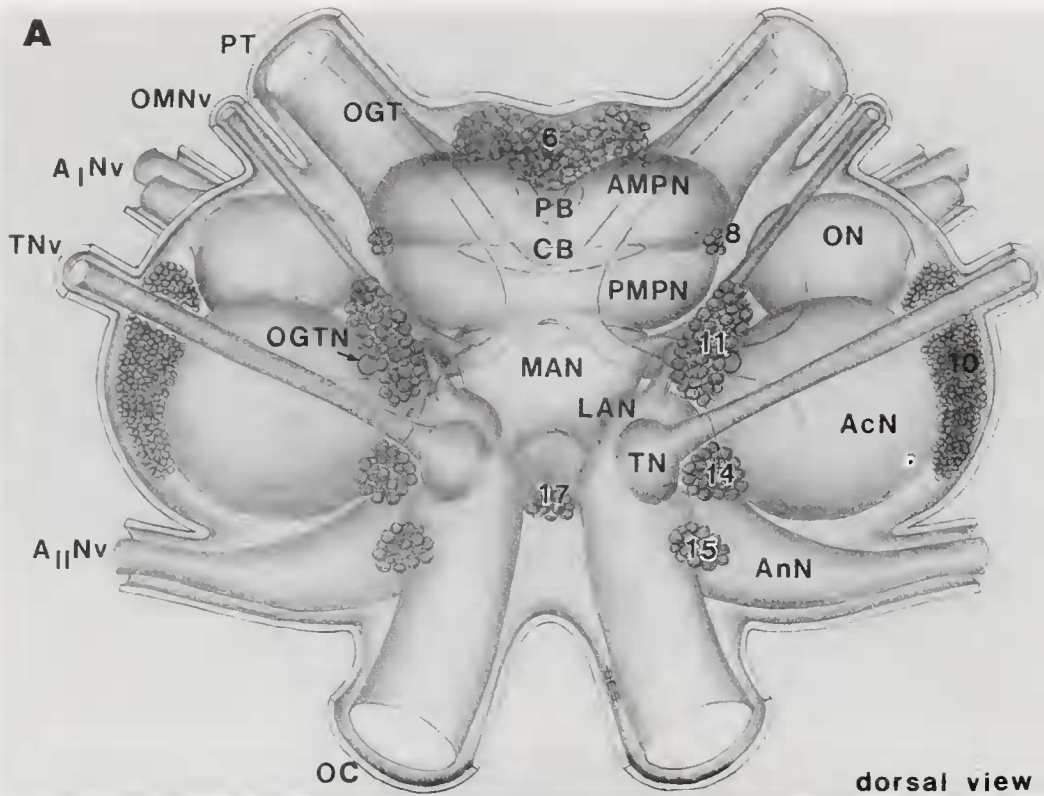
Figure 3A, B. Graphic reconstruction of the neuropils and cell clusters in dorsal and ventral views of the brain of the crayfish. This figure, and those for the crab and spiny lobster, were reconstructed from sectioned material, so that the proportions of the brain areas and positions of the cell clusters are reasonably accurately retained. The numbers and size of the cell bodies shown, however, do not represent the true situation, apart from indicating the difference between the characteristically small "globuli" cells associated with the accessory and olfactory lobes, and the larger cell bodies found elsewhere in the brain. A key to the abbreviations is provided in Appendix 2. See text for details.
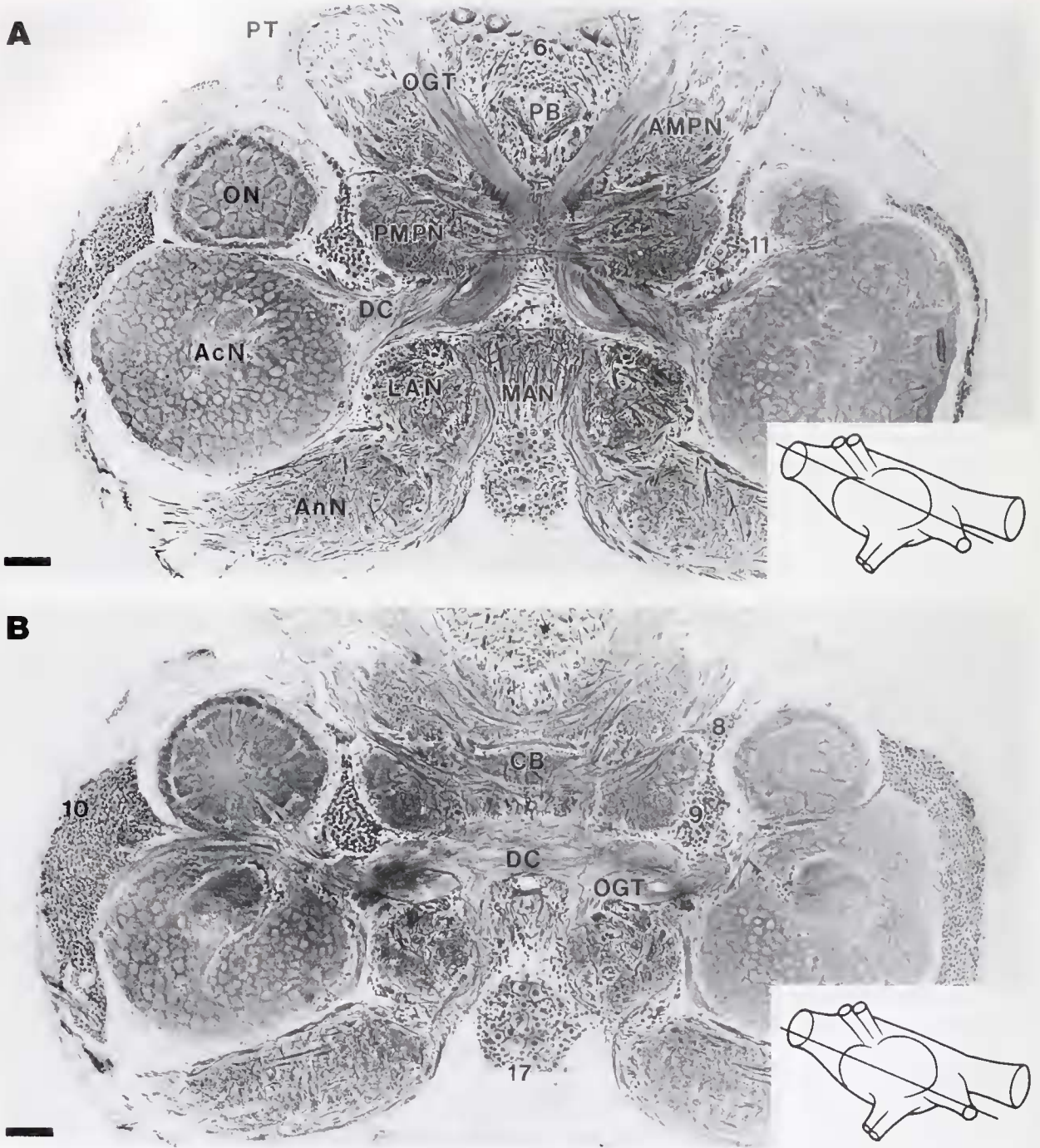
Figure 4.   Horizontal sections of the brain of *Cherax*. In this and in the following figures, the planes of the sections are indicated on the inset diagram which shows the brain in side view with anterior on the left. Figure 4A includes the olfactory globular tract (OGT) which forms a chiasm at the center of the brain and then diverges to end in the olfactory (ON) and accessory (AcN) lobes. All the main neuropils can be seen in this plane. Figure 4B is a section through a more ventral plane and shows the deutocerebral commissure (DC) extending across the brain between the two accessory lobes. A and B show how the olfactory globular tract passes dorsally over the deutocerebral tract in the midline and then ventrally beneath it before entering the olfactory and accessory lobes. Scale bars = 100 μm.
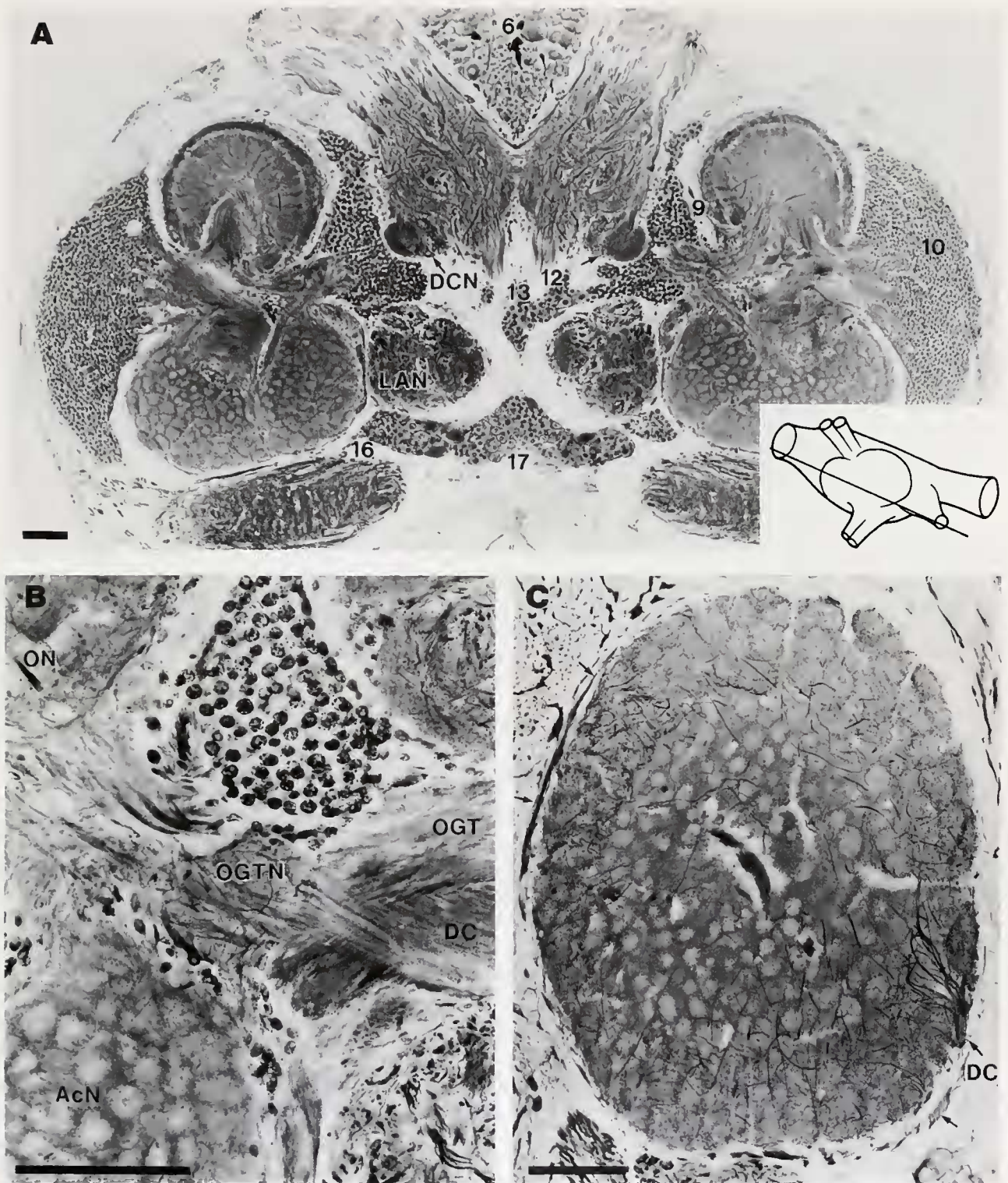
Figure 5. A. A horizontal section near the ventral surface of the *Cherax* brain. At this level the ventrally situated deutocerebral neuropils can be seen (DCN). The medial antenna I neuropil is no longer in the plane of the section, but the lateral antenna I neuropils (LAN) are still present as round areas, medial to the accessory lobes. Bundles of axons at their anterior margins are the beginning of the antenna I nerve root. The olfactory lobes are enclosed by the fine fibers of the axons from the chemoreceptors. These axons are also contained in the antenna I nerve root. B. The small olfactory globular neuropil (OGTN) contained within the fibers of the olfactory globular tract (OGT) at the point where the olfactory globular tract and the deutocerebral commissure (DCN) cross before projecting to the neuropils to the olfactory (ON) and accessory lobes (AcN). C. Darkly stained axons (arrows) from the deutocerebral tract (DC) penetrate the accessory lobe from the periphery to end in two layers of glomeruli in the lobe. Scale bars = 100 μm.
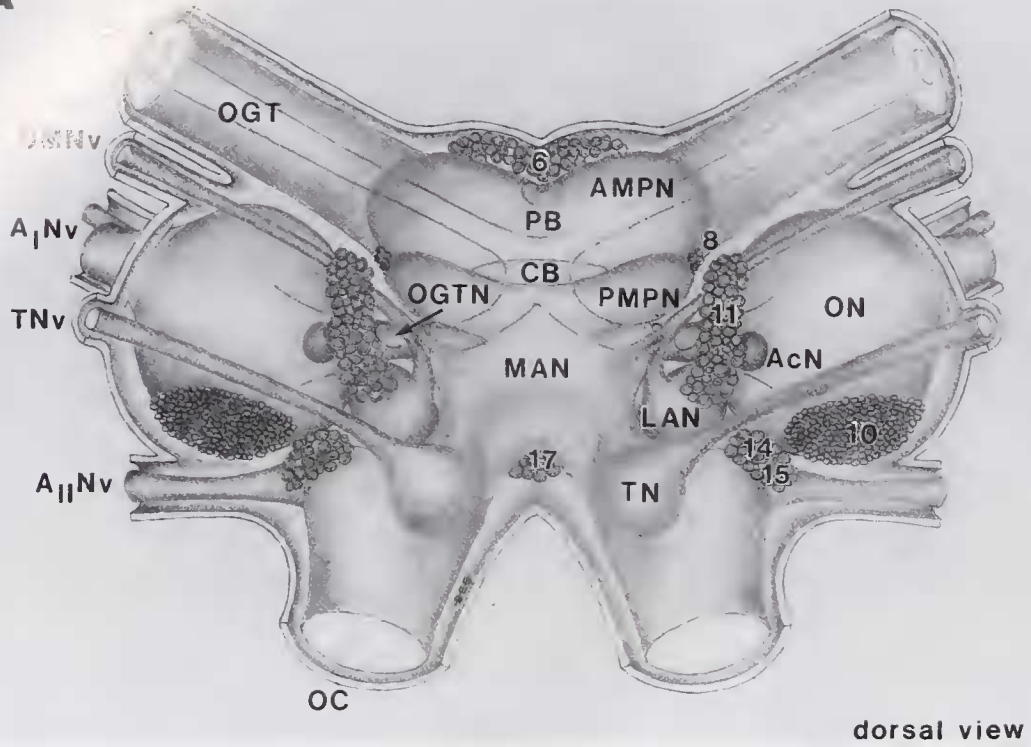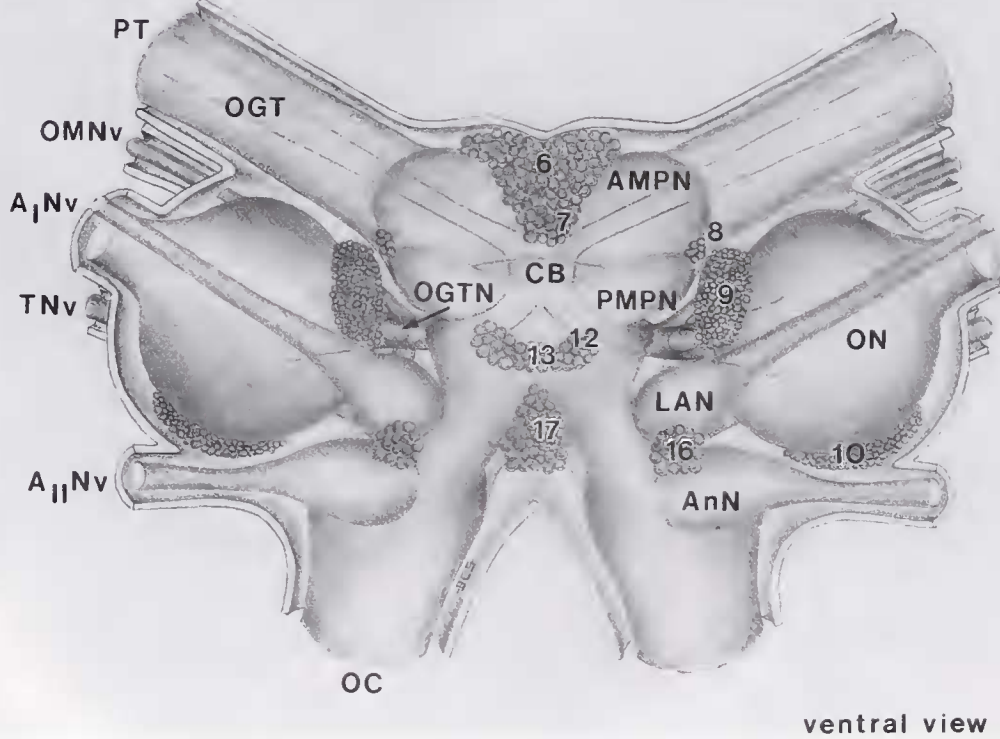
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Figure 6A, B.   Dorsal and ventral views of the brain of *Scylla serrata* as an example of a brachyuran. See text for details.
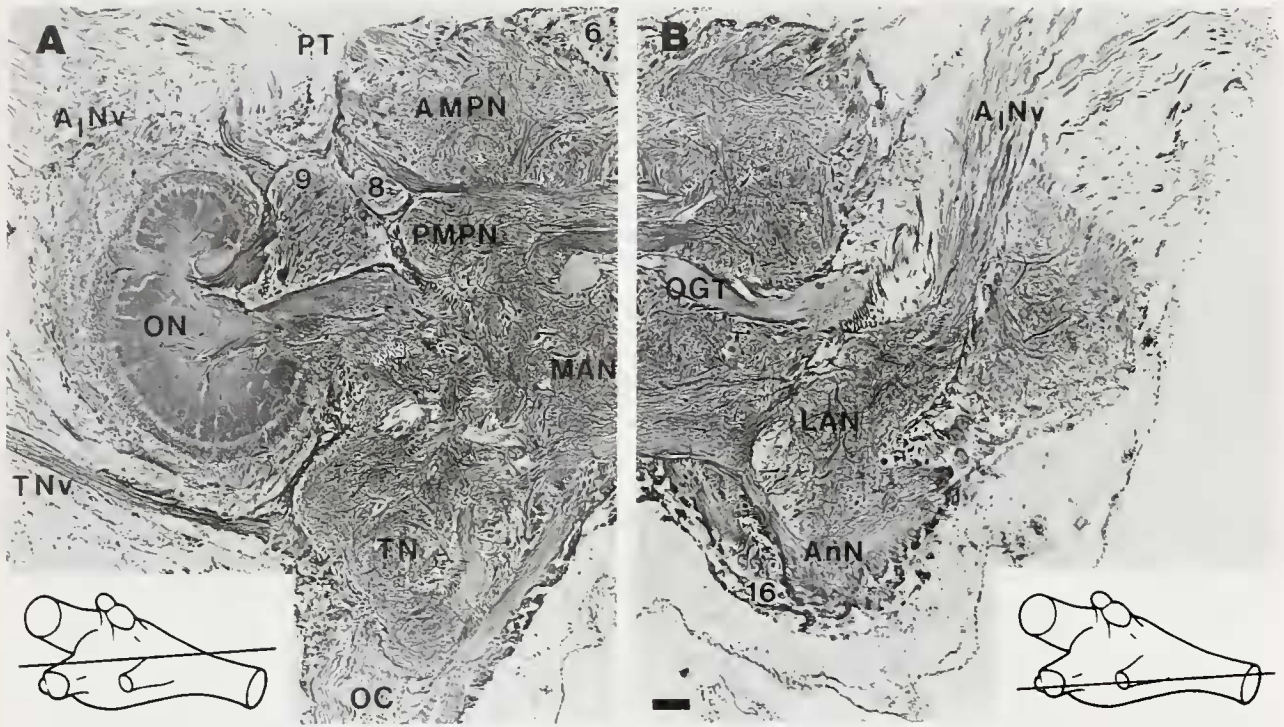
Figure 7. A horizontal section through the brain of *Scylla*. This section is slightly oblique, passing through more dorsal neuropils on the left (A) and more ventral neuropils on the right (B). The anterior medial protocerebral neuropils (AMPN) are larger than the posterior protocerebral neuropils. The olfactory lobes (ON) are also large and enclosed by many chemoreceptive fibers projecting from the antennules in the antenna I nerve root. The tegumentary nerve root and neuropil are prominent (A), whereas the lateral antenna I neuropil and the antenna II neuropil are relatively small (B). Scale bar = 100 μm.

The cell bodies are contained in clusters; some of these clusters are clearly recognizable in all brain types, some are not. In previous studies, cell body clusters have been given specific names, and these names differ from one brain type to another. Here, we describe the cell clusters according to the brain region in which they are found. In this way we avoid functional names for cell clusters that may be highly heterogeneous and that may contain the cell bodies of neurons with widely differing functions and projections.

We recognize 17 different clusters of cell bodies that appear to be common to all brain types; to simplify matters we have numbered the cell clusters, 1–17, from anterior to posterior. Tables in Appendix 1 provide cross references to the descriptions provided in this paper and by previous authors.

Protocerebrum[†]

OPTIC GANGLIA. In the optic ganglia we recognize (1) cell bodies that lie distal to the lamina, (2) cell bodies that

lie distal or adjacent to the external medulla, and (3) cell bodies that lie adjacent to the internal medulla, or between the internal and terminal medulla.

Detailed information about the projections of many of the cell bodies in the optic ganglia is available for some crustaceans (Nässel, 1977; Sandeman, 1982).

LATERAL PROTOCEREBRUM. The lateral protocerebrum contains (4) cell bodies that lie adjacent to the terminal medulla, and (5) cell bodies that lie adjacent to the hemiellipsoid body.

Detailed information about the projections of some of the cell bodies in the lateral protocerebrum of spiny lobsters and crayfish is available (Blaustein *et al.*, 1988; Derby and Blaustein, 1988).

MEDIAN PROTOCEREBRUM. The median protocerebrum includes (6) a prominent medial cluster of cell bodies, some of which are very large; lying around the front of the brain and extending from the dorsal to ventral surfaces; (7) lateral cell bodies that may appear in some preparations as extensions of cell cluster 6 on the ventral surface of the brain and in others as separate groups; and (8) small lateral groups of cell bodies that lie on either side of the central body at the junction be-
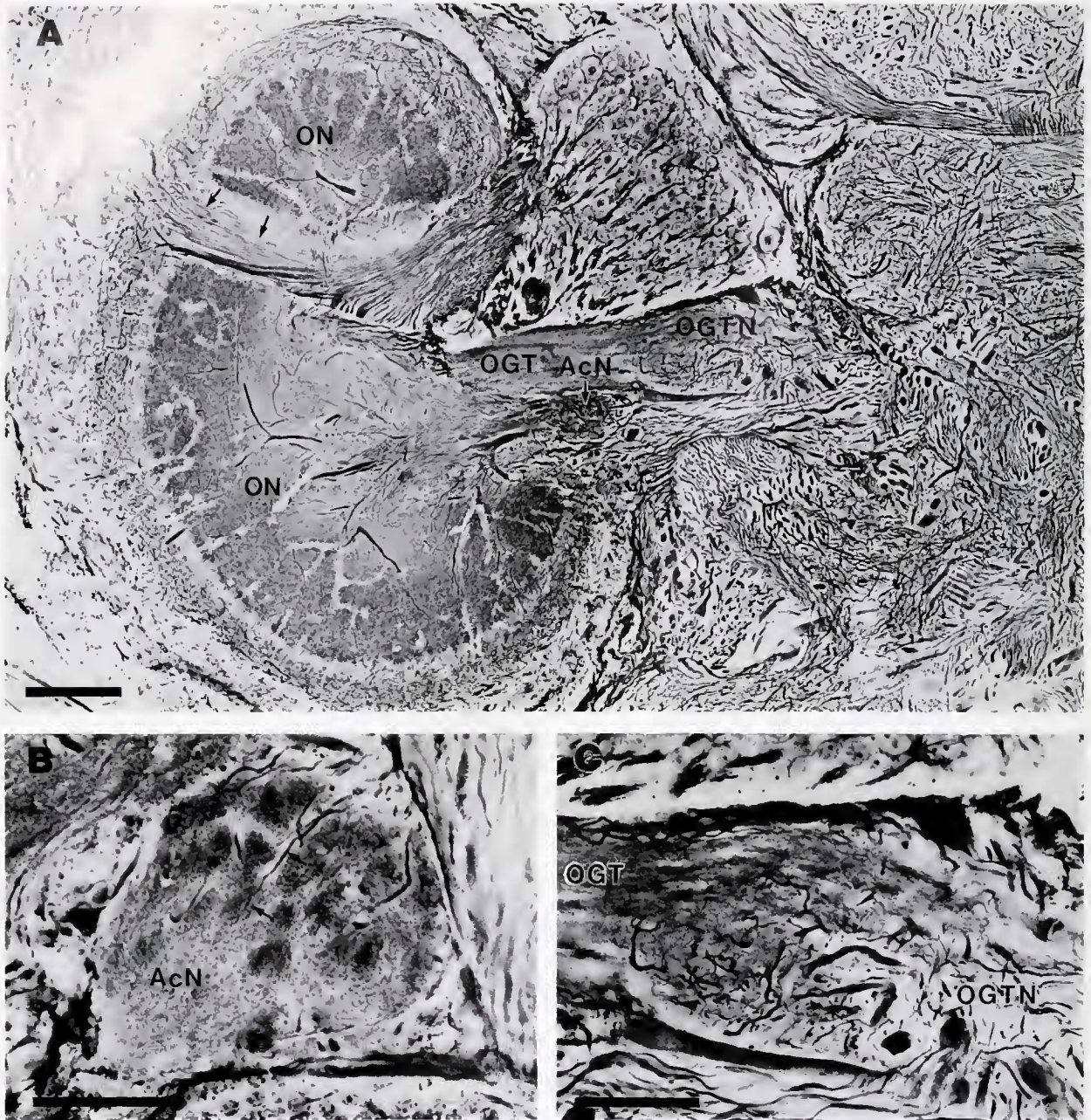
Figure 8.   A. Horizontal section through the brain of *Scylla* (left side) showing the location of the olfactory globular tract neuropil (OGTN) and the small accessory lobe (AcN). Primary neurites (arrows) from the medial globuli cells in crabs pass through the neuropil of the olfactory lobe and spread out over its periphery. B. The reduced accessory lobe of crabs retains its glomerular structure and receives darkly staining axons (arrows) that end in the glomeruli. C. The olfactory globular tract neuropil is contained amongst the fibers of the olfactory globular tract. Scale bars = 8A, 100 μm; 8B = 25 μm; 8C = 50 μm.

tween the anterior and posterior medial protocerebral neuropils. These are subdivided in spiny lobsters.

Deutocerebrum

The cell bodies of the deuterocerebrum are recognized as follows: (9) Laterally situated, characteristically small cell bodies with nuclei that almost fill the cell lumen, lying ventrally between the anterior medial margin of the olfactory lobe and the posterior medial protocerebral neuropil, or ventral to the posterior part of the olfactory lobe. The primary neurites of these cells are directed towards the olfactory (and, when present, accessory) lobes.
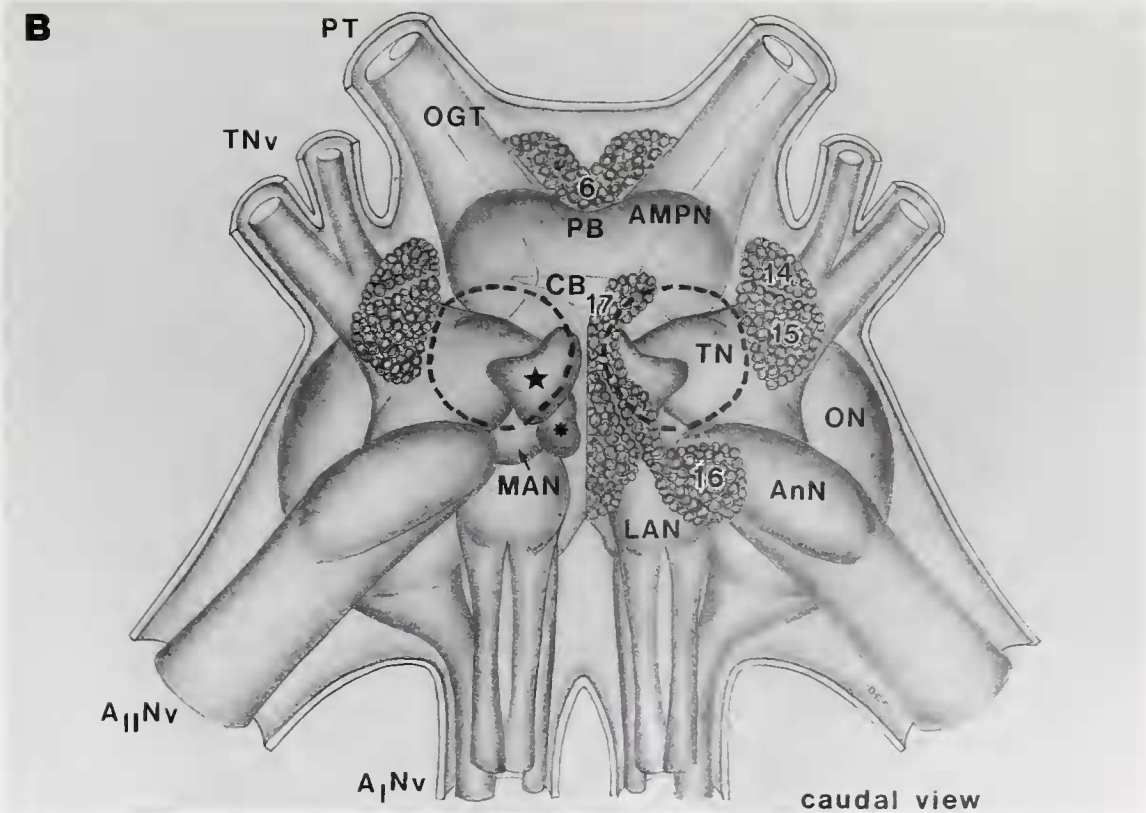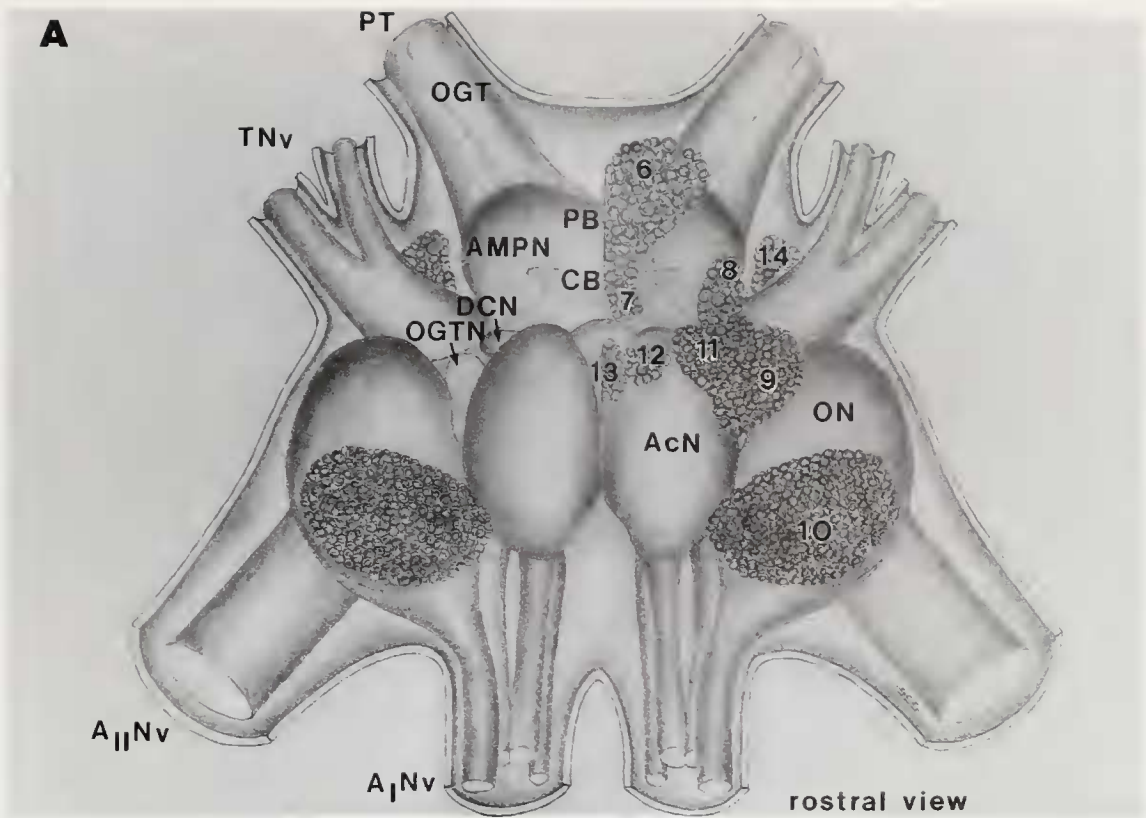
Figure 9A, B. Rostral and caudal views of the brain of *Panulirus argus* as an example of a palinuran. Medially placed cell bodies in the drawings of *Panulirus* have been shown only on one side to avoid obscuring the underlying neuropil areas. See text for details.
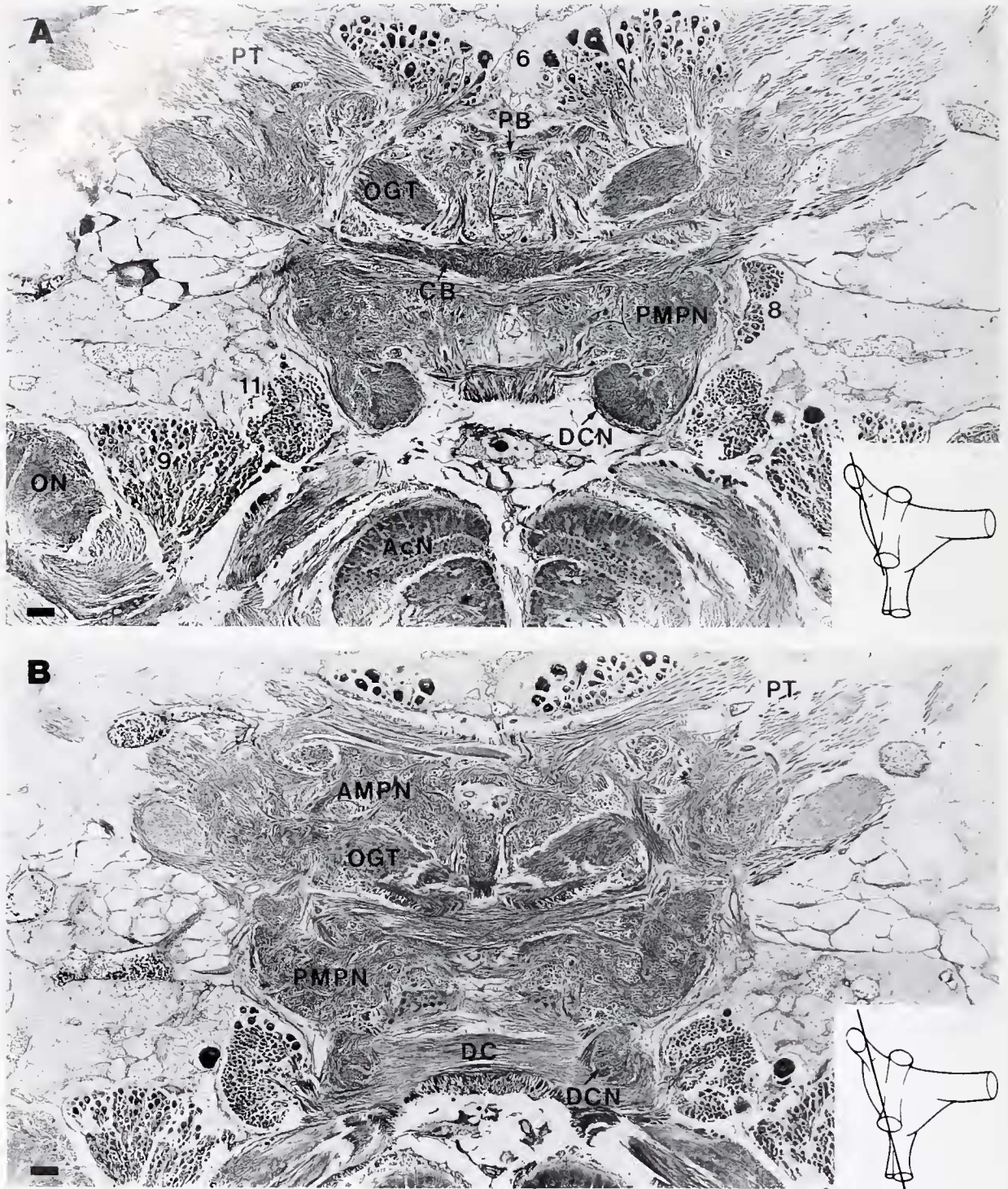
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Figure 10.   A. A frontal section passing through the medial protocerebral neuropils of *Jasus* and showing the location of the protocerebral bridge and central body (CB). The olfactory globular tracts (OGT) lie near the surface of the protocerebral tracts (PT) and in this section are converging on the center of the brain where they will form a chiasm. The deutocerebral neuropils (DCN) lie ventral to the posterior medial protocerebral neuropil (PMPN) as they do in *Cherax*. B. Further into the brain (equivalent to moving more dorsally in *Cherax*) the deutocerebral commissure (DC) can be seen with its connections to the deutocerebral commissure neuropils (DCN). Scale bars = 100 μm.

(10) Like the cell bodies of cell cluster 9, these are also small with nuclei that nearly fill the lumen. In the crayfish where the accessory lobe lies directly posterior to the olfactory lobe, these cell bodies constitute a large lateral group. In spiny lobsters, where the accessory lobes lie medial to the olfactory lobes, and in the crabs where the accessory lobes are very small, the above cell bodies lie posterior to the olfactory lobes. (11) A heterogeneous, laterally placed group, containing small and large cell bodies. They occupy the space between the olfactory lobes and the median antenna 1 neuropils on the dorsal side of the deutocerebrum. They are contiguous with cell cluster 10 in spiny lobsters. (12) Laterally situated cells, similar in makeup to cell cluster 11 and occupying about the same antero-posterior position, but lying on the ventral surface of the brain. (13) A medial group of cell bodies, lying on the ventral surface, and fused with cell cluster 12 in crabs and spiny lobsters.

Tritocerebrum

The following cell clusters are recognized in the tritocerebrum: (14) Small laterally situated groups of cell bodies lying over the anterior medial margin of the antenna II neuropil on the dorsal side of the brain. (15) A small laterally situated group of cells lying over the posterior medial margin of the antenna II neuropil on the dorsal side of the brain. Often fused with cluster 14. The primary neurites of cell bodies in 14 and 15 end in the antenna II neuropils in crayfish (Sandeman, unpub. obs.). (16) Laterally situated cell bodies on the ventral surface of the brain that lie directly below the anterior margins of the antenna II neuropil. Although they occupy a relatively caudal position in the brain, the primary neurites of virtually all these cell bodies extend to the deutocerebrum in the spiny lobster (Schmidt, unpub. obs.). (17) A medial cluster of cell bodies of different sizes, grouped between the oesophageal connectives, and spreading from the dorsal to the ventral surface of the brain and thence out over the ventral surface of the brain.

Brain Plans of the Different Infraorders

The shapes, and an indication of the relative sizes of the brains of the crayfish, crab, and spiny lobster, seen from the side and above, are shown in Figure 2. The folded nature of the spiny lobster brain, with the dorsally extending protocerebral tracts and ventrally projecting antenna 1 and antenna II nerve roots, is well demonstrated in side view.

Astacura (clawed lobsters and crayfish *e.g., Homarus, Procambarus, Astacus, Orconectes, Cherax, Euastacus, Pacifastacus*). The crayfish *Cherax destructor* has been used as an example of an astacuran brain. A dorsal view

of the brain is shown in Figure 3A, and a ventral view in Figure 3B. Micrographs of horizontal sections taken through different planes are shown in Figures 4 and 5. The brain regions (proto-, deuto-, and tritocerebrum) lie almost in a single plane, so that most of the neuropils can be seen in both dorsal and ventral views.

The protocerebral tracts (PT) enter the anterior medial protocerebral neuropils (AMPN) antero-laterally. Enclosed within the neuropils of the median protocerebrum are the protocerebral bridge (PB) (Fig. 4A) and the central body (CB) (Fig. 4B). The olfactory globular tract (OGT) is also buried within the neuropils, but comes close to the dorsal surface where the protocerebral tracts enter the median protocerebrum (Fig. 4A).

The deutocerebrum is dominated by the laterally situated olfactory (ON) and accessory (AcN) lobes that are the origin of the olfactory globular tract. The small olfactory globular tract neuropils (OGTN) are embedded within the olfactory globular tract close to the point where it branches into the olfactory and accessory lobes (Fig. 5B). The deutocerebral commissure runs between the two accessory lobes and has strong projections to the deutocerebral commissure neuropil (DCN) on the ventral side of the brain (Figs. 4B, 5A). Axons from the deutocerebral commissure enclose the accessory lobe (AcN) and penetrate from the periphery of the lobe to end in glomeruli lying in two layers in the lobe (Fig. 5C). Fine axons from olfactory sensilla on the antenna 1 end in the olfactory lobe (Fig. 5A). No projections from peripheral sense organs or motor neurons have been described in the accessory lobes.

The lateral (LAN) and median (MAN) antenna 1 neuropils are located medial to the olfactory and accessory lobes (Figs. 4A, 5A). Axons in the antenna 1 nerve (A_1Nv) and in the oculomotor nerve (OMNv) both originate or end in these two neuropils. Axons in the oculomotor nerve also project to the posterior medial protocerebral neuropils (PMPN).

The tritocerebrum contains the tegumentary (TN) and antenna II (AnN) neuropils which receive inputs from the receptors on the carapace and antenna II, respectively. The motorneurons controlling the movements of antenna II are located in the antenna II neuropil.

Clusters of cell bodies are clearly delineated in the crayfish. The cell bodies associated with the olfactory and accessory lobes (9 and 10) are characteristically small with nuclei that almost fill the cell lumen. Cluster 10 is located laterally, a situation not shared with the crabs and spiny lobsters.

Brachyura (crabs; *e.g., Scylla, Carcinus, Callinectes, Hemigrapsus, Leptograpsus*). The crab *Scylla serrata* is taken as an example of a brachyuran. A dorsal view of the brain is shown in Figure 6A and a ventral view in
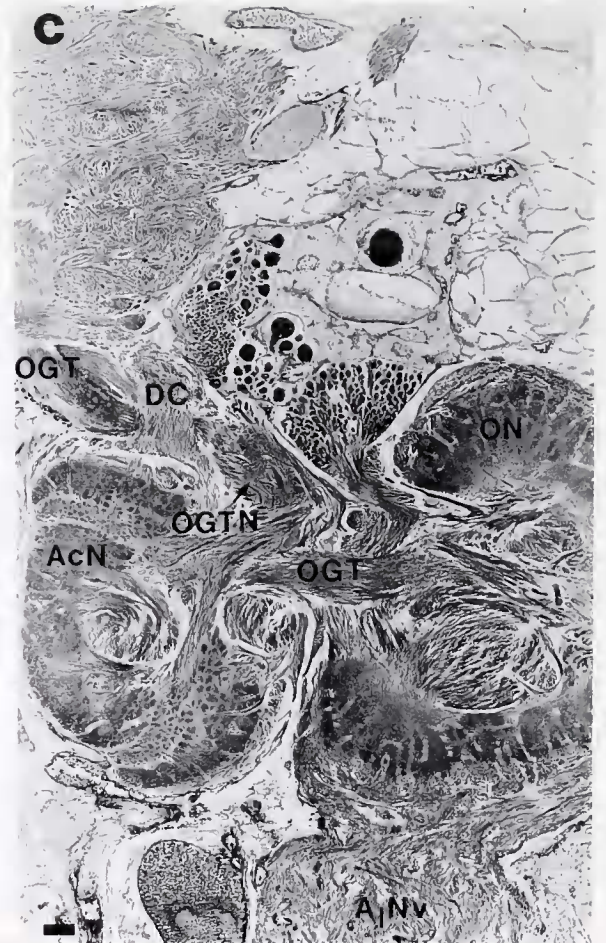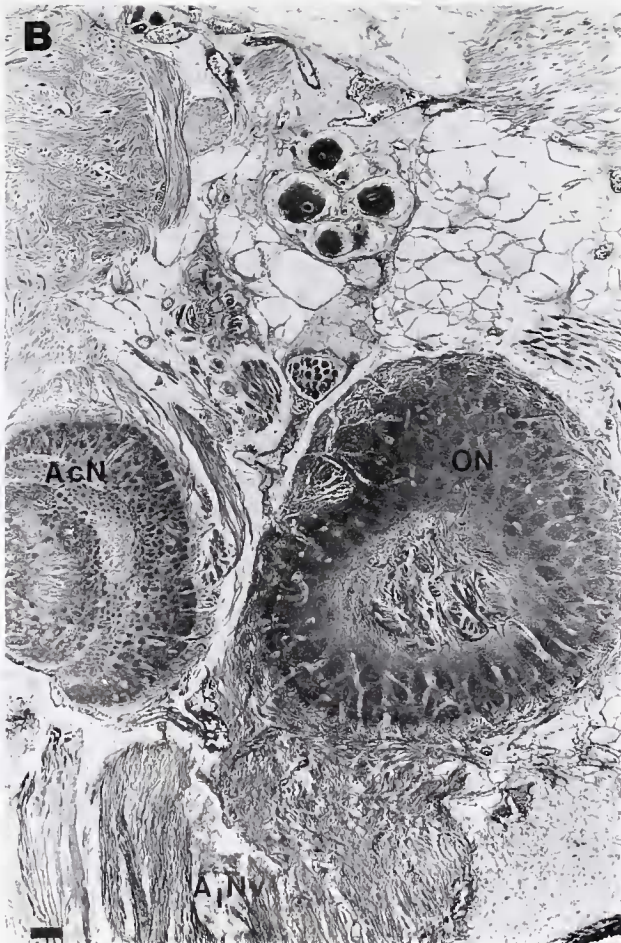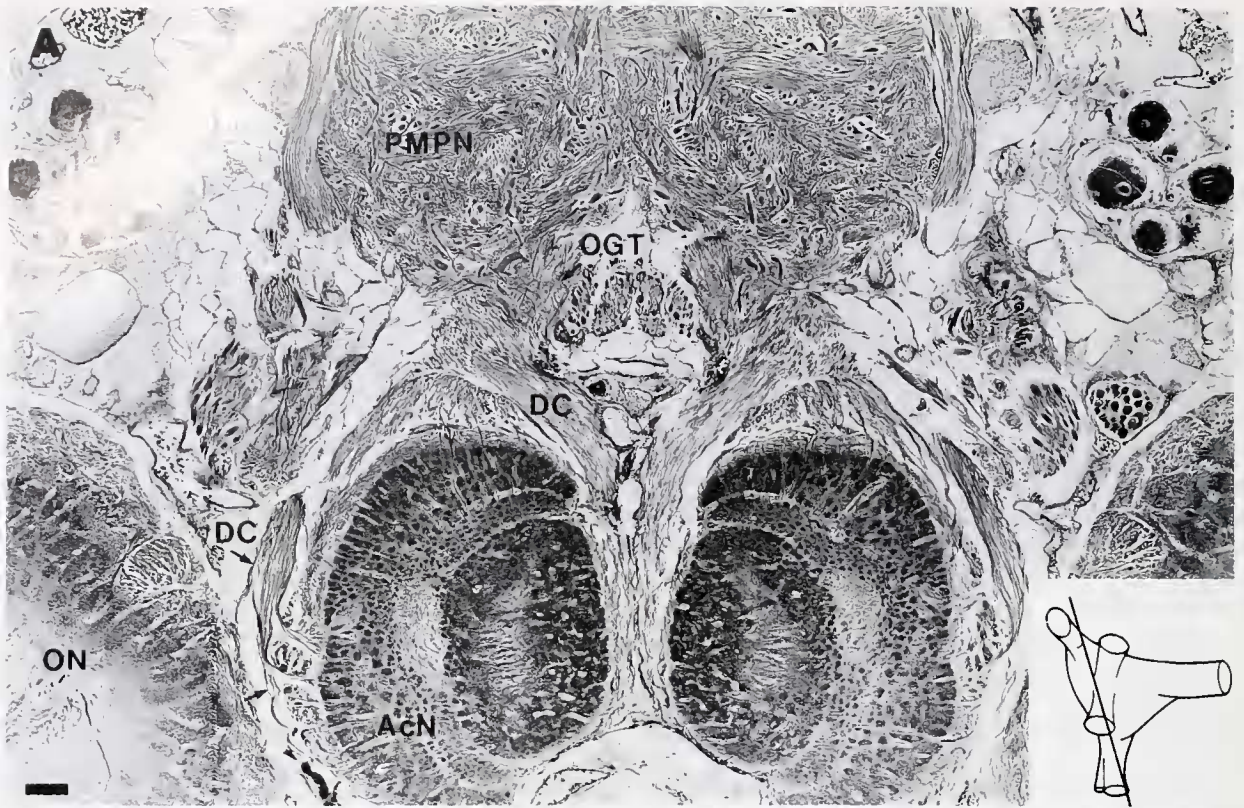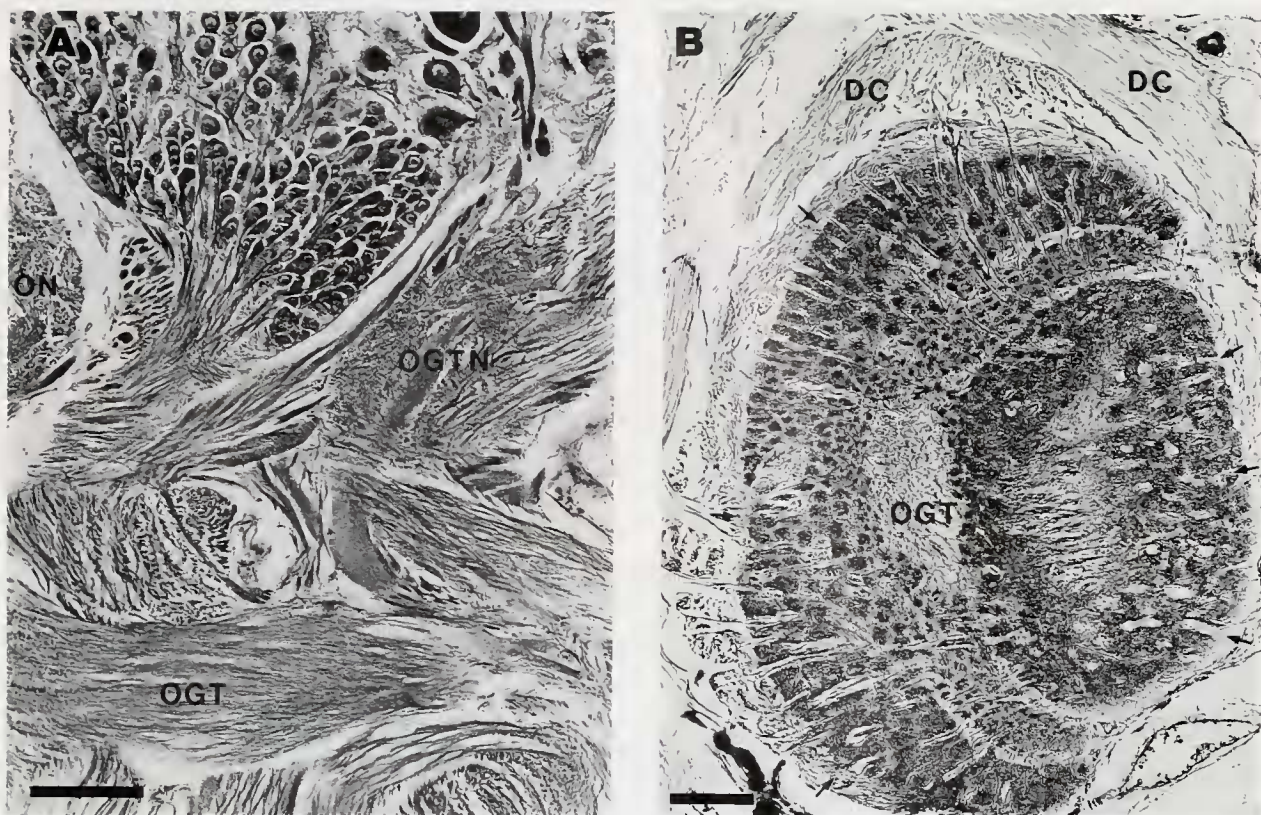
Figure 12. A. The olfactory globular tract neuropil on the left side of the brain of *Jasus*. As in the crayfish and crab, this neuropil is formed from arborizations among the fibers of the olfactory globular tract, just before it diverges into the olfactory and accessory lobes. B. The accessory lobe of *Jasus* has three layers of glomeruli, the outer two being cup shaped and the inner layer forming a spherical area of neuropil enclosed by the other two. Axons from the deutocerebral commissure (arrows) that enter from the lateral surfaces appear to reach all layers, whereas those that enter medially appear to stop within the central area of neuropil. Fine fibers from the olfactory globular tract (OGT) that enter the glomerular layers from within the lobe can be seen in the figure. Scales bars = 100 μm.

Figure 6B. Like the crayfish, the three brain regions of the crab brain lie in one plane so that most of the neuropils can be seen from both sides.

The protocerebral tracts are large in brachyurans and contain a number of axons of a large diameter. The anterior medial protocerebral neuropils (AMPN) are also proportionately larger than in crayfish. The protocerebral bridge (PB), central body (CB), and the olfactory globular tract (OGT) are not different from those of crayfish; they occupy the same sites and are similarly proportioned (Fig. 7).

Two features in the deutocerebrum distinguish the brachyuran brain from the crayfish (and spiny lobster). First, there is a marked reduction in the size of the accessory lobes (AcN). These are tucked in at the posteromedial edge of the olfactory lobes (ON). They are small but retain their glomerular structure (Fig. 8A, B). Second, a large deutocerebral commissure and the associated deu-

Figure 11. A. The large accessory lobes (AcN) are medial to the olfactory lobes (ON) in the palinurans. Axons in the deutocerebral commissure (DC) sweep around the olfactory globular tract and descend over the accessory lobes containing three layers of glomeruli. B. The right half of the brain of *Jasus* showing the axons from chemoreceptors on the antennule ascending and enclosing the laterally placed olfactory lobe (ON). Axons to the left of those projecting to the olfactory lobe end in the lateral antennal 1 neuropil. Both sets of axons are contained in the antenna I nerve root. C. A section through the center of the olfactory (ON) and accessory lobes (AcN) to show the branches of the olfactory globular tract (OGT) axons to both accessory and olfactory lobes. The olfactory globular tract neuropil (OGTN) lies close to where the olfactory globular tract enters the two lobes. Scale bars = 100 μm.
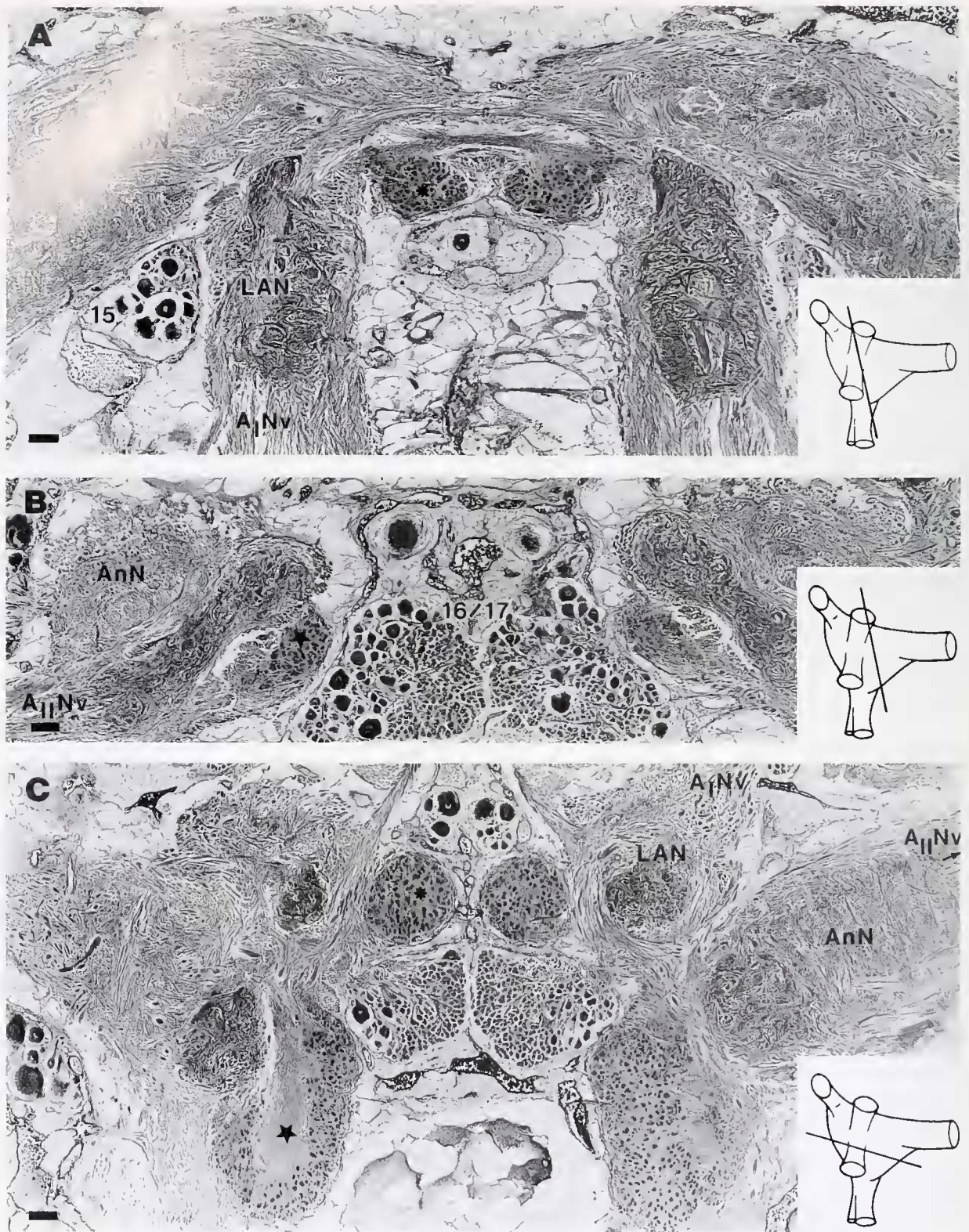
Figure 13. A. A frontal section of *Jasus* brain passing through the lateral antenna I neuropils (LAN) and the antenna II neuropils (AnN). Axons in the antenna I nerve root (A$_I$Nv) ascend from below to enter the lateral antenna I neuropil. The antenna II nerve roots (A$_{II}$Nv) enter the brain more laterally. The two areas of glomerular neuropil (asterisk) that lie between the lateral antenna I neuropils are the antennular glomeruli reported by Blaustein *et al.*, 1988, and are unique to spiny lobsters. B. A section taken further caudal to that shown in A passes through the caudal extremities of the antenna II neuropil

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tocerebral neuropils have not yet been determined, although the axons that project to the accessory lobes do cross the brain and pass ventral to the olfactory globular tract at the midline. The olfactory globular tract neuropil (OGTN) (Fig. 8C) is present. The absence of a large accessory lobe results in the cell body cluster 10 occupying a position posterior to the olfactory lobe, instead of lateral to it as in the crayfish.

The lateral (LAN) and medial (MAN) antenna I neuropils are located medial to the olfactory lobes and are the origin or destination of motor and sensory neurons in the antenna I (A_INv) and oculomotor (OMNv) nerves (Fig. 7).

There is little difference between the tritocerebrum of the crayfish and the crab. The tegumentary nerve (TNv) in the crab ends in its neuropil (TN) which lies on the dorsal surface of the brain at the base of the oesophageal connectives. The antenna II neuropil (AnN) is proportionately smaller in the crab than in the crayfish, but occupies the same position. The second antennae of the crabs are also much smaller than those of the crayfish.

Clusters of cell bodies in the crab brain are very similar to those in the crayfish, with the exception of cluster 10 which has far fewer cell bodies than either the crayfish or spiny lobster and, as in the lobster, is located posterior to the olfactory lobe.

Palinura (spiny lobsters, slipper lobsters; *e.g., Jasus, Panulirus, Arctides, Ibacus*). Two lobsters, *Jasus novae-hollandiae* and *Panulirus argus*, have been used here to represent the palinuran brain. Two characteristic features of the palinuran brain are present in all members of the group, namely a rotation of the medial protocerebral neuropils back over the deutocerebrum so that they come to lie dorsal to it, and the location of the large accessory lobes medial to the olfactory lobes. The upwardly folded median protocerebrum of the spiny lobster makes the "dorsal" and "ventral" views that are shown for the crayfish and crab less useful in depicting the spiny lobster brain morphology. For this reason the views that are shown are rostral (from in front) in Figure 9A and caudal (from behind) in Figure 9B. Dorsal is, therefore, at the top of the page, and ventral at the bottom in these figures.

The protocerebral tracts (PT) enter the anterior median protocerebrum (AMPN) dorso-laterally, and the protocerebral bridge (PB), central body (CB), and olfactory globular tract (OGT) can be found in the same places as in the other two brain types (Fig. 10A). The posterior medial protocerebral neuropils (PMPN) are hidden in the

rostral view by the deutocerebral neuropils and by the tritocerebral neuropils in the caudal view.

The dominant deutocerebral neuropils are the olfactory (ON) and accessory (AcN) lobes and can be seen best in the rostral view. Quite unlike the organization in the crayfish, the four neuropils are lined up and thrust forward with the olfactory lobes flanking the medially located and slightly smaller, accessory lobes (Fig. 11A). The antenna I nerve (A_INv) projects ventrally (in the plane of the page in Fig. 4) and contains bundles of axons that end or originate in the lateral (LAN) and median (MAN) antenna I neuropils, or in the olfactory lobes (ON) (Fig. 11B, C). No projections from any nerve roots have been found that end in the accessory lobe. A large deutocerebral commissure connects the two accessory lobes, and axons from this project to the deutocerebral commissure neuropil (DCN) (Fig. 10A, B), also visible in the rostral view. As in crayfish, axons from the deutocerebral commissure penetrate the accessory lobe from the perimeter and end in spherical glomeruli. There are three layers of glomeruli in the spiny lobster accessory lobes, and the penetrating axons end in all (Fig. 12B). The olfactory globular tract, as in crayfish, branches into both the accessory and olfactory lobes (Figure 11C), and a small neuropil, the olfactory globular tract neuropil (OGTN) is associated with the tract just before the branch point (Figs. 11C, 12A).

The lateral (LAN) and median (MAN) antenna I neuropils are partly obscured by the tritocerebral neuropils, but can be seen in the caudal view. Two neuropils associated with the deutocerebrum in the spiny lobsters may be unique to those animals. These have been called the antennal and antennular glomeruli (Fig. 13) (Blaustein *et al.*, 1988). They are indicated in Figures 4B and 13A, B, C by a star and an asterisk respectively and have not been identified in the other two brain types.

The caudal view of the brain (Fig. 4B) shows how its folded nature brings the median protocerebrum to lie dorsal to the tritocerebral neuropils. The large tegumentary nerve (TNv) projects dorsally from the large tegumentary neuropils (TN) on the dorsal side of the tritocerebrum, close to the base of the oesophageal connectives. These project towards the observer in Figure 4B, and their positions are shown by two dashed circles. The antenna II neuropils (AnN) lie ventral to the oesophageal connectives as in the other two brain types, and the very large antenna II nerves (A_{II}Nv) project ventrolaterally.

Identification of the cell body clusters in the spiny lob-

and through a second pair of glomerular neuropil areas (star), the antennal glomeruli (Blaustein *et al.*, 1988), also unique to the spiny lobsters. (C) The antennular (asterisk) and antennal (star) glomeruli, and their relationship to the neuropils of the lateral antenna I and antenna II, can be clearly seen in a horizontal section through this area of the brain. Scale bars = 100 μm.

ster is less certain than in the other two brain types. The cells associated with the olfactory and accessory lobes are easily identified by their characteristically small size and large nuclei. Cluster 10, found lateral to the olfactory and accessory lobes in crayfish, are posterior to the olfactory lobes in the spiny lobster. Other cell clusters, such as 6, 7, 8, 11, and 17, are relatively certain to be homologues of the same clusters in the other two brain types. Less certain are the clusters 14, 15, and 16, and the large cluster adjacent to 17 which spreads out over the ventral surface of the brain between the lateral antenna 1 neuropils.

Discussion

In proposing a standard nomenclature for the components in the brains in three infraorders of the decapod crustaceans, we set out with the assumption that the same neural components (neuropils, tracts, cell clusters) would be represented in all three members of this phylogenetically close grouping. This has proved to be largely true, with the exception of the two deutocerebral neuropils in the spiny lobsters, the antennal and antennular glomeruli. These may either represent a special development of the spiny lobster, or the homologous areas in the crab and crayfish have not yet been recognized. The organization of the optic ganglia is remarkably constant within the three groups, perhaps because few degrees of freedom are allowed in a neuropil designed to compute the direction and velocity of images moving across the receptors of the retina.

If, as suggested by the similarity of the optic ganglia, common function leads to common neural structure, then the relative size of a neuropil area in the crustacean brain could be a reflection of the dominance of a particular sensory modality, as is the case with fish that live in clear or turbid water (Huber and Rylander, 1992). The brachyurans, for example, have large protocerebral tracts and large medial protocerebral neuropils, suggesting a reliance on the visual system. The second antennae are relatively small and the antenna II neuropil is also correspondingly reduced when compared with the crayfish and the spiny lobster. The spiny lobsters and crayfish brains are dominated by the antenna I and antenna II neuropils, olfactory lobes, and above all, accessory lobes. From what we know of the behavior of these animals they are night active and must rely heavily on tactile and olfactory senses.

To follow up these and other questions related to the brain and behavior in the crustaceans requires a much more precise knowledge of the brain neuroanatomy than what is presented here or known at the present stage. There is very little information, for example, about the connectivity between neuropils in the crustacean brains, and not even the function of the accessory lobe, central body, and protocerebral bridge have been understood. The demonstration of homologous neuronal components in the three brain types enhances the value of comparative studies and the establishment of a common nomenclature is a useful first step in this direction.

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Appendix 1

The first listed and underlined name is the one we have preferred. Equivalents are listed below each preferred name. References indicate studies in which the names have been used but not necessarily the origin of the name.

Brain Divisions and Neuropils

Optic ganglia: (Kirk *et al.*, 1983; Titova, 1985; Tsvileneva and Titova, 1985; Blaustein *et al.*, 1988).
= optic lobes: (Sandeman and Luff, 1973; Nässel and Elofsson, 1987)
= optic masses: (Hanström, 1925)

Lamina: (Strausfeld and Nässel, 1980; Sandeman, 1982; Siwicki and Bishop, 1986)
= lamina ganglionaris: (Hanström, 1931, 1947; Bullock and Horridge, 1965; Maynard, 1966; Hafner, 1973; Elofsson, 1983; Kirk *et al.*, 1983; Siwicki and Bishop, 1986; Sandeman *et al.*, 1988; Blaustein *et al.*, 1988)
= optic lamina: (Hamori and Horridge, 1966)

External medulla: (Hanström, 1931, 1947; Bullock and Horridge, 1965; Sandeman, 1982; Elofsson, 1983; Siwicki and Bishop, 1986; Sandeman *et al.*, 1988; Blaustein *et al.*, 1988)
= medulla externa: (the above authors also use the latin version)
= medulla: (Strausfeld and Nässel, 1980; Kirk *et al.*, 1983; Nässel and Elofsson, 1987)

Internal medulla: (Hanström, 1931, 1947; Bullock and Horridge, 1965; Sandeman, 1982; Elofsson, 1983; Siwicki and Bishop, 1986; Sandeman *et al.*, 1988; Blaustein *et al.*, 1988)
= medulla interna: (the above authors also use the latin version)
= lobula: (Strausfeld and Nässel, 1980; Kirk *et al.*, 1983; Nässel and Elofsson, 1987)

Terminal medulla: (Hanström, 1931, 1947; Bullock and Horridge, 1965; Sandeman, 1982; Elofsson, 1983; Siwicki and Bishop, 1986; Sandeman *et al.*, 1988; Blaustein *et al.*, 1988)
= medulla terminalis: (the above authors also use the latin version)
= lobula plate: (Strausfeld and Nässel, 1980)

Hemiellipsoid body: (Hanström, 1931; Bullock and Horridge, 1965; Sandeman, 1982; Blaustein *et al.*, 1988)
= corpora pendunculata (Hanström, 1924, 1925)
= globuli (Hanström, 1925)

Anterior medial protocerebral neuropil:
= anterior optic neuropil: (Bullock and Horridge, 1965; Sandeman, 1982; Sandeman *et al.*, 1988; Blaustein *et al.*, 1988)
= anterior and lateral optic neuropil: (Titova, 1985; Tsvileneva and Titova, 1985)
= dorsal anterior and ventral optic neuropil: (Helm, 1928)

Posterior medial protocerebral neuropil:
= posterior optic neuropil: (Bullock and Horridge, 1965; Sandeman, 1982; Sandeman *et al.*, 1988; Blaustein *et al.*, 1988)
= posterior protocerebral neuropil: Tsvileneva and Titova, 1985)
= medial optic neuropil: (Helm, 1928)

Protocerebral bridge: (Helm, 1928; Bullock and Horridge, 1965; Sandeman, 1982; Tsvileneva and Titova, 1985; Sandeman *et al.*, 1988)

Central body: (Helm, 1928; Bullock and Horridge, 1965; Sandeman, 1982; Tsvileneva and Titova, 1985; Sandeman *et al.*, 1988)

Olfactory lobe: (Helm, 1928; Hanström, 1925, 1931, 1947; Bullock and Horridge, 1965; Sandeman, 1982; Tsvileneva and Titova, 1985; Sandeman *et al.*, 1988; Ache and Schmidt, 1988; Mellon and Munger, 1990)
= hemiglobulus anterior and posterior: (Bethe, 1897)

Lateral antenna 1 neuropil:
= lateral antennular neuropil: (Hanström, 1924; Helm, 1928; Sandeman, 1982; Titova, 1985; Tsvileneva and Titova, 1985; Sandeman and Sandeman, 1987; Sandeman *et al.,* 1988; Blaustein *et al.,* 1988)
= parolfactory lobe: (Hanström, 1947; Bullock and Horridge, 1965; Maynard, 1966; Sandeman and Luff, 1973; Sandeman, 1982; Tautz and Müller-Tautz, 1983; Yoshino *et al.,* 1983; Siwicki and Bishop, 1986; Nässel and Elofsson, 1987; Arbas *et al.,* 1988)

Median antenna 1 neuropil:
= medial antennal neuropil: (Bullock and Horridge, 1965; Sandeman, 1982; Tsvileneva and Titova, 1985; Sandeman and Sandeman, 1987; Blaustein *et al.,* 1988)

Accessory lobe: (Helm, 1928; Hanström, 1931, 1947; Bullock and Horridge, 1965; Sandeman, 1982; Tsvileneva and Titova, 1985; Sandeman and Sandeman, 1987; Sandeman *et al.,* 1988; Blaustein *et al.,* 1988)
= lobus accessorius (Hanström, 1925)
= neuropilum parvum: (Bethe, 1897)

Deutocerebral commissure neuropil:
= parolfactory lobe: (Titova, 1985; Tsvileneva and Titova, 1985; Sandeman and Sandeman, 1987; Sandeman *et al.,* 1988; Blaustein *et al.,* 1988)
= lateral glomeruli: (Mäynard, 1966; Sandeman, 1982)
= paracentral lobe: (Hanström, 1947;
= nebenlappen: (Hanström, 1924, 1925)
= uv neuropil: (Helm, 1928; Sandeman, 1982)

Olfactory globular tract neuropil:
= "z" neuropil figured by Hanström (1928). Also referred to by Tsvileneva and Titova (1985); Sandeman and Sandeman (1987); Sandeman *et al.,* (1988); Schmitt *et al.,* (1991)

Antenna II neuropil:
= antennal neuropil: (Bullock and Horridge, 1965; Taylor, 1975; Sandeman and Wilkens, 1982; Tsvileneva and Titova, 1985)
= antennary neuropil: (Helm, 1928; Sandeman, 1982)

Tegumentary neuropil: (Bethe, 1897; Helm, 1928; Sandeman, 1982; Tsvileneva and Titova, 1985)

Antennular glomeruli: (Blaustein *et al.,* 1988)

Antennal glomeruli: (Blaustein *et al.,* 1988)

Tracts and Commissures

Optic tract:

Protocerebral tract: (Tsvileneva and Titova, 1985; Sandeman *et al.,* 1988)
= optic tract: (Hanström, 1924; Bullock and Horridge, 1965; Sandeman *et al.,* 1975)

= optic nerve: (Wiersma *et al.,* 1964; Sandeman, 1964, 1982)

Olfactory globular tract: (Helm, 1928; Bullock and Horridge, 1965; Tsvileneva and Titova, 1985)
= tractus optico-globularis (Bethe, 1897)
= tractus optico-antennularis (Hanström, 1924)
= tractus olfactorio-globularis (Hanström, 1925)

Deutocerebral commissure: (Titova, 1985; Tsvileneva and Titova, 1985; Sandeman and Sandeman, 1987; Sandeman *et al.,* 1988; Blaustein *et al.,* 1988)
= antennular commissure: (Hanström, 1925; Sandeman, 1982)
= olfactory commissure: (Bullock and Horridge, 1965)

Oesophageal connectives: (Sandeman and Luff, 1973; Sandeman, 1982; Nässel and Elofsson, 1987; Sandeman *et al.,* 1988)
= circumoesophageal connectives: (Helm, 1928; Siwicki and Bishop, 1986; Blaustein *et al.,* 1988)
= pharyngeal connectives: (Hanström, 1924, 1947)

Cell Bodies

The cell body clusters have been given different names by different authors. As explained in the text, we identify 17 clusters of cell bodies. Our identifying number is given in the first column (Ref) in the following tables and can be used to determine, across the tables, which cell body clusters are homologous.

*Blaustein and Derby (1988) (*Procambarus *and* Panulirus*)* (The first column of abbreviations refers to *Procambarus,* the second to the analogous cell clusters in *Panulirus*)

Ref.	Cluster name	Abbreviation	
1.	—	—	
2.	—	—	
3.	—	—	
4.	Cell cluster C,D,E,F	C,D,E,F	C,D,E,F
5.	Cell cluster A,B,G	A,B,G	A,B,G
6.	Anterior cluster	AC	AC
7.	Anterior cluster	AC	AC
8.	Ventral paired anterior cluster	VPAC	VPALC
9.	Ventral paired lateral cluster	VPLC	VPMLC
10.	Lateral cluster	LC	VPPLC
11.	Dorsal anterior cluster	DAC	VPMLC
12.	Ventral paired medial cluster	VPMC	VPMC
13.	Ventral unpaired medial cluster	VUMC	VUMC
14.	Dorsal medial clusters	DMC	DPMC

15. Dorsal posterior clusters	DPC	DUMC
16. Ventral paired anterior clusters	VPPC	DUMC
17. Ventral unpaired posterior cluster	VUPC	DUMC

Tautz and Müller-Tautz (1984)

Ref.	Cluster name	Abbreviation
1.	—	
2.	—	
3.	—	
4.	—	
5.	—	
6.	Anterior cluster	ac
7.	Ventral paired anterior cluster	vpac
8.	—	
9.	Ventral paired lateral cluster	vplc
10.	Lateral cluster	lc
11.	Dorsal anterior cluster	dac
12.	Ventral paired medial cluster	vpmc
13.	Ventral unpaired medial cluster	vumc
14.	Dorsal medial cluster	dmc
15.	Dorsal posterior cluster	dpc
16.	Ventral paired posterior cluster	vppc
17.	Ventral unpaired posterior cluster	vupc

Sandeman (1982) (after Helm 1928) (Helm's nomenclature is included in parenthesis)

Ref.	Cluster name	Abbreviation
1.	—	
2.	—	
3.	—	
4.	—	
5.	—	
6.	Anterior medial cells (cellulae anteriores)	I
7.	Anterior medial cells (cellulae anteriores)	I
8.	Dorsal lateral cells (cellulae superiores laterales)	II
9.	Ventral lateral cells (included in the cellulae superiores laterales)	IV
10.	Olfactory lobe cells (cellulae lobi olfactorii)	III
11.	Dorsal lateral cells (cellulae superiores laterales)	II
12.	Anterior medial cells (cellulae anteriores)	I
13.	Anterior medial cells (cellulae anteriores)	I
14.	Posterior lateral cells (cellulae angulares)	V
15.	Posterior lateral cells (cellulae angulares)	V
16.	Posterior medial cells (cellulae posteriores)	VI
17.	Posterior medial cells (cellulae posteriores)	VI

Appendix 2

Abbreviations used in this paper:

APPENDAGES
ANT I: antenna I
ANT II: antenna II

NERVE ROOTS
AMNv: anterior median nerve
OMNv: oculomotor nerve
A_INv: antenna I nerve
A_{II}Nv: antenna II nerve
TNv: tegumentary nerve
PMNv: posterior median nerve

NEUROPILS
L: lamina
EM: external medulla
IM: internal medulla
TM: terminal medulla
HN: hemiellipsoid body
AMPN: anterior medial protocerebral neuropil
PMPN: posterior medial protocerebral neuropil
PB: protocerebral bridge
CB: central body
ON: olfactory lobe
LAN: lateral antenna I neuropil
MAN: median antenna I neuropil
AcN: accessory lobe
DCN: deutocerebral commissure neuropil
OGTN: olfactory globular tract neuropil
AnN: antenna II neuropil
TN: tegumentary neuropil

TRACTS AND COMMISSURES
OT: optic tract
PT: protocerebral tract
OGT: olfactory globular tract
DC: deutocerebral commissure
OC: oesophageal connectives